

When the Beachhopper Looks at the Moon: The Moon-Compass Hypothesis

JAMES T. ENRIGHT
Scripps Institution of Oceanography

THE DISCOVERY BY VON FRISCH AND KRAMER that honey bees and starlings are able to use the position of the Sun to orient in a fixed compass direction seemed highly improbable when initially described. Subsequent research, however, has borne out these claims and demonstrated that many other animals, both vertebrate and invertebrate, have the same capacity. Sun-compass orientation now represents one of the most secure foundation blocks underlying the hypotheses proposed to account for otherwise unexplainable cases of animal orientation and navigation.

Shortly after this remarkable discovery, two Italian workers, Pardi and Papi, published substantial evidence indicating that crustacean sandhoppers, amphipods of the genus *Talitrus*, are also able to use Sun-compass orientation, with a directional preference that would be seaward on the beach from which the animals were collected (ref. 1); and advanced the claim, on less extensive evidence, that these amphipods can also use the position of the Moon in order to orient toward the shoreline, in a manner similar to their performance with the Sun (ref. 2). Moon-compass orientation of this sort would be a phenomenon even more remarkable

than Sun-compass orientation, because of the complex pattern from hour to hour and day to day in the direction of the Moon. It is surprising, then, that so little subsequent research on Moon-orientation has been undertaken to verify or disprove this claim.

A possible explanation for this lack of interest may be that the Moon-compass hypothesis is an intrinsically unattractive proposition. As applied to talitrids, the hypothesis requires the assumption that the amphipods have two separate and independent timing mechanisms: a Sun-clock, synchronized by the day-night cycle, which the animal consults when orienting by the Sun; and a Moon-clock, which operates at a slightly slower rate, which is synchronized by other environmental stimuli, and which the animal consults when orienting by the Moon. The amphipod would, then, not behave as a temporal unit, with internal synchronization of various functions, but instead must be assumed to have two time-measuring systems, much as a railroad conductor might have two separate watches, one in each pocket, to use when crossing to different time zones. For me, then, the Moon-compass hypothesis is esthetically unappealing.

Nevertheless, I will be presenting extensive evidence that seems to favor the Moon-compass hypothesis. But let me reemphasize at the outset that this is not because I like the hypothesis. The reason for this anomalous position in which I find myself is that there now exists an appreciable body of data on nocturnal orientation of talitrids, data that require explanation. Although the Moon-compass hypothesis is an esthetically unattractive way of explaining these data, it seems to me to be the best of the alternatives presently available.

The evidence bearing on the Moon-compass hypothesis that I propose to review consists of the data from five published papers (ref. 2, hereafter designated as San Rossore I experiments; ref. 3: San Rossore II experiments; ref. 4: La Jolla experiments; ref. 5: Castiglione experiments; and table 1¹ of ref. 6: Mogadiscio experiments); a manuscript by Peter Craig (Univ. of California, Santa Barbara),² which he has very kindly sent to me before publication (Santa Barbara experiments); and the data from two extensive studies of my own that have not previously been published (Naples and Malibu experiments). These latter data are summarized in detail in appendixes A and B and constitute a larger number of experiments than the total contained in all the published literature. I will draw upon all of these data in an attempt to answer a series of questions of increasing complexity about the nocturnal behavior of talitrids.

Methods and Materials

The procedure used in studies of Moon orientation has consisted of collecting groups of amphipods from the beach, usually during the daylight hours, at which time they are buried at depths of 2 to 20 cm into the sand; storing them in light-tight containers until

the start of observation (exceptions in ref. 4²); placing them into a circular, sealed observation chamber, in which a view of terrestrial landmarks is prevented; and recording their positions—the directions of orientation—as they aggregate around the margin of the container.

About 25 animals have been used per experiment. In all published experiments, the animals have been stored in bottles containing sand; removal of the animals from the sand for transfer to the orientation chamber requires several minutes of exposure to moonlight. In the Naples and Malibu experiments (appendixes 1 and 2), I kept the animals before observation in sealed containers in which there was only a strip of paper towel, moistened with seawater; this permits transfer to the orientation chamber within a matter of seconds after removal from darkness.

Craig and I have photographed the animal positions with the camera above the observation chamber, through a glass cover; Papi, Pardi, and Ercolini have photographed the animals from beneath, or, in one study (some of the Mogadiscio experiments) made visual counts of position. In most cases, the orientation chamber has been heated to about 20° C, and in some cases, also dehydrated; the possible influence of these experimental conditions is discussed in detail in question VII below.

¹The other data in ref. 6 are derived from performances when the Moon was passing through the zenith or culminating in the north. The orientations observed were usually widely scattered, with only eight results statistically significant. The orientations also deviated by large amounts from the expected direction, a fact which the authors attribute to peculiarities in lunar path on the equator during the equinox. For this reason data in tables 2 and 3 of ref. 6 may not represent a valid test of the Moon-compass hypothesis.

²CRAIG, P. C.: An Analysis of the Concept of Lunar Orientation in *Orchestoidea corniculata* (Amphipoda). In press, *Animal Behavior*, 1971.

All of my experiments have been conducted in locations far from the possible influence of urban illumination. Apparently only the Mogadiscio experiments were conducted within a large city, and the experimenters, in that case, have described the precautions they took to reduce the influence of urban lighting to a diffuse glow (ref. 6, p. 229).

The direction of orientation of the animals within an experiment has been averaged by a vectorial method (ref. 1, p. 463) that is now widely used in orientation studies. In addition to its direction, this vector has a length that can range from zero to one and measures the internal agreement in the experimental observations, with a short vector indicating a wide scatter in the positions of the animals.

The experimental organisms have included three species of talitrid amphipods: *Talitrus saltator* (San Rossore, Castiglione and Naples experiments), *Orchestoidea corniculata* (La Jolla, Malibu and Santa Barbara experiments), and *Talorchestia martenisii* (Mogadiscio experiments). Although these are members of different genera, their morphology and choice of habitat would lead the non-specialist to regard them as very closely related and ecologically equivalent. In my opinion, none of the differences between the data sets to be evaluated can unequivocally be traced to a difference between species; greater differences in nocturnal orientation have been recorded within a species than between species.

SURVEY OF DATA

Question 1

Do the amphipods usually show significant, non-random choices of direction at night when deprived of all obvious orientational clues except the Moon and stars?

A rigorous evaluation of non-randomness in the data from Moon-orientation experiments is a complex statistical problem because all observations have been made with groups of 10 to 40 animals placed simultaneously in a relatively small container. The amphipods often push and crawl over each other, so that their choices of position cannot legitimately be regarded as independent. All statistical tests for the significance of orientation, however, assume a series of independent observations. This disparity between experimental methods and statistical requirements means that the probability levels which can be derived from a statistical test cannot be regarded as completely legitimate; the probability that a given distribution could arise by chance alone may well be underestimated.

In addition, one must be particularly careful about the degrees of freedom applicable to the statistical test, since several of the published sets of data (San Rossore II, Castiglione, Mogadiscio) are derived from repetitive photographs of the same group of animals. A proper, conservative approach requires that the nonrandomness of a particular distribution of directions of orientation be assessed on the basis of the numbers of animals observed and not on the numbers of positions recorded. I have excluded all directions of orientation by talitrids from further data analyses in which a statistical test on the basis of the number of animals used indicates that the orientation was not significantly non-random at the 5-percent level³ or better. (See appendix 3 for a list of published data which have been so excluded.) This precaution seems essential to assure that the data on observed directions of orientation are not

³ Statistical significance has been evaluated by means of figure 15 of Schmidt-Koenig (ref. 7). Because of the interactions between animals the quoted levels of significance must be regarded as doubtful.

badly distorted by chance factors, or perhaps due only to chance. I have also used only those data from the Mogadiscio experiments which were based on photographs, except when the photographic observation was not statistically significant, in which case I used the data from the succeeding visual count (See appendix 4). This restriction of the usable data is not primarily because of any doubts about the reliability of visual counting of moving animals, but because internal evidence in the data implies that the visual counts were usually made on the same group of amphipods that had just previously been photographed. In that case, the visual counts would not represent independent data in a rigorous sense but only the equivalent of additional photographs of the same animals.

Even after making allowances for all these complications, however, there are sufficient data now available to indicate that talitrid amphipods do, indeed, very often show conspicuous nonrandomness in their orientation at night when they can see the Moon. Table 1 contains a summary of the proportion of experiments in which the observed orientation was strong enough to be considered significant (with reservations; see footnote 3) at the 0.01 level. In several of the experimental series additional cases involved strong suggestions of orientation ($0.01 < p^3 < 0.05$), so that the available data to assess the directions of orientation are somewhat greater than the numbers of cases indicated as positive in this table. The internal consistency of the directions chosen by separate groups of animals, when significant orientation was observed within an experimental series (discussed below), lends further emphasis to the conclusion that nonrandom orientation is involved.

An appreciable number of experiments have been performed, however, in which the observed animal positions are not distinguish-

TABLE 1.—Cases of Non-Random Orientation

| Experimental series | Number of experiments | Percentage of experiments showing strong orientation ($p < .01$) ^a |
|------------------------------|-----------------------|---|
| San Rossore I. | 16 | No data on scatter |
| San Rossore II | | |
| Freshly collected | 17 | 100 |
| Kept 11 to 20 days | 17 | 65 |
| La Jolla | | |
| Freshly collected | 37 | 89 |
| Kept 1 or 2 weeks | 15 | 47 |
| Castiglione | | |
| Freshly collected | 11 | 100 |
| Mogadiscio | | |
| Freshly collected | 34 | 56 |
| Santa Barbara | | |
| Freshly collected | 59 | 29 |
| Naples | | |
| Freshly collected | 25 | 68 |
| Kept 3 to 10 days | 42 | 57 |
| Malibu | | |
| Freshly collected | 44 | 82 |
| Kept 2 to 5 days | 36 | 72 |

^a See footnote 3 in text.

able from a random distribution even at the 5-percent level of significance: cases in which the animals scattered in all directions. As suggested by the breakdowns in table 1, animals kept in the laboratory for longer periods of time apparently show random scatter in their directions more often than freshly collected animals; and, as will be considered subsequently, clearer evidence for orientation is often obtained at full Moon than at other times. Nevertheless, there remain many cases—particularly in the data of Craig, but also in other experimental series—in which a scatter not distinguishable from a random choice of directions has been observed and for which no adequate explanation seems available. In

my opinion, the best reply to the question posed in this section is that talitrid amphipods are very often able to orient significantly when they see the Moon, but that they sometimes do not, for unknown reasons.

Question II

Is the Moon the primary orienting stimulus in these experiments, when clear orientation is observed?

The principal evidence available for the conclusion that the amphipods use the Moon for orientation consists of data from mirror experiments: the animals are permitted to view the Moon while they orient; then the view of the Moon is obstructed by a screen, and its image is reflected onto the orientation chamber by means of a mirror from some new direction. Relatively few mirror experiments have been performed, and the results of these tests are not entirely satisfying.

If the Moon is the sole orienting stimulus, one could well expect that the animals would orient toward the mirror with an angle corresponding to that which they assume relative to the real Moon. This has been recorded in some experiments but less convincingly so in others.

The best performance of amphipods in a series of mirror experiments is found in my data for *Talitrus saltator* from Naples (fig. 1A). In these experiments, the mirror sometimes reflected the Moon's image from an altitude of about 30° and in other cases, an altitude of about 60° . Apparently only lunar azimuth affected orientation. Another clearly positive result was obtained in a single experiment with *Orchestoidea corniculata* in my La Jolla experiments (fig. 1B).

Papi and Pardi's results (ref. 2) with *Talitrus saltator* showed a wide scatter (fig. 2A and B), but it is uncertain to what extent these particular results should be a cause for

concern, since no data were given on the number of animals used or the degree of scatter within the observations. My results from mirror experiments in the Malibu experimental series also showed large departures from expectations (fig. 2C and D). There was, in these latter experiments, also, a strong trend for the amphipods' orientations toward reflected moonlight to be more dispersed than their orientations toward the Moon itself. All observations included in figure 2C and D are statistically significant ($p < .01$; see footnote 3), but the vector length within the mirror experiments was smaller (i.e., the scatter was greater) than in the preceding control experiment with the Moon itself in 19 cases out of 24.

A single experiment of another sort per-

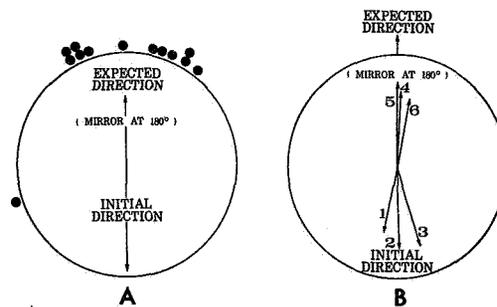


FIGURE 1. "Successful" mirror experiments: (A) Data from Naples experiments, April 3, April 8, and April 13, 1963; direction of orientation initially assumed by the animals has been used for standardization (downward); image of Moon was reflected from a direction opposite the actual lunar azimuth. Each small circle represents orientation observed in a separate experiment; (B) Sequence of observations from mirror experiment of La Jolla series. Arrows represent vectors, lengths of which are proportional to unit radius of the large circle. Numbers refer to sequence in which observations were made; 1, 2 and 3 represent orientation with the Moon visible; 4, 5 and 6 represent orientation to image of Moon reflected from a mirror at 180° from lunar azimuth (after Enright, ref. 4).

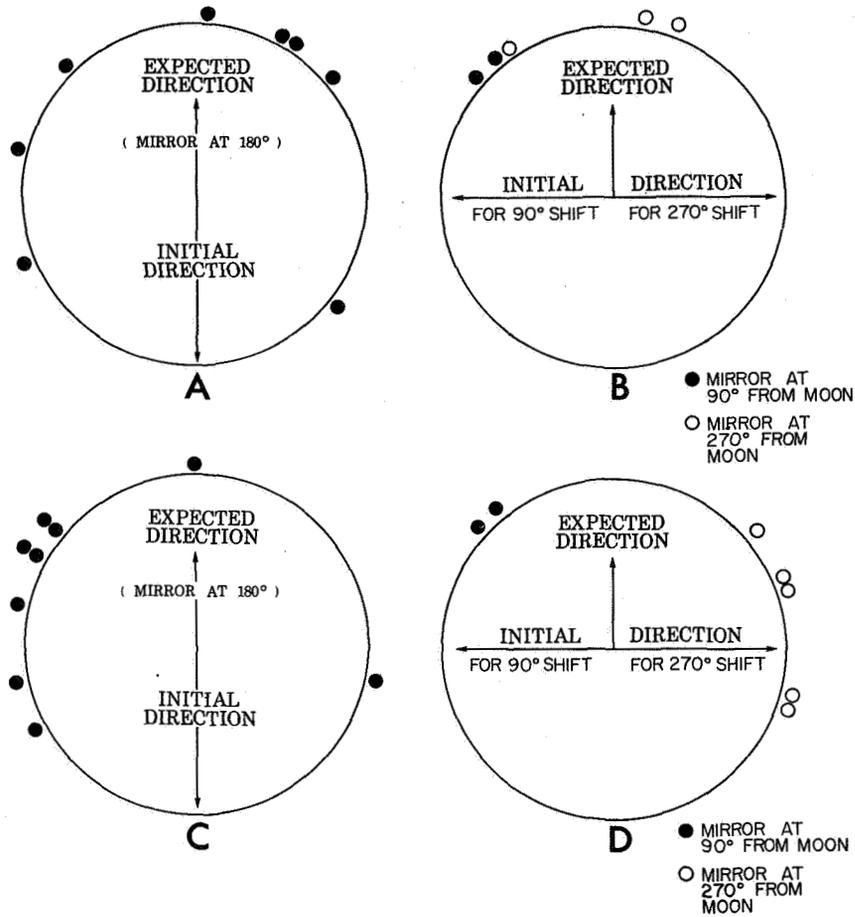


FIGURE 2. Less successful mirror experiments. All orientations standardized relative to initial orientation, so that "expected" direction is upward. Each small circle represents results from a separate experiment. (A) and (B): Data from ref. 2; (C) and (D): Data from Malibu experiments, October 17, 1964.

formed as part of this series seems to me to be of broader significance, and I offer my apologies that this result has not been documented by many repetitions. Following initial orientation with a view of the Moon, and several relatively successful mirror experiments, the animals were left undisturbed in the orientation chamber for 10 minutes, during which time a direct view of the Moon was obstructed, and then their distribution

was recorded, still with the Moon hidden. As is evident in table 2, the amphipods which could not see the Moon or its reflection showed strong orientation in a direction not greatly different from that observed when they could see the Moon.

This result was initially very disconcerting; it leads to serious questions about whether moonlight is, indeed, the factor responsible for the orientation. It brought to

my attention, however, the following fact: obstructing a direct view of the Moon by means of an opaque screen 1 m wide located 2 to 3 m from the observation chamber does not provide the animals with a stimulus-free visual environment, any more than it would during the daytime. In addition to the form of the Moon itself, moonlight includes the illumination of a broad region of the sky, and it was very easy to determine the brightest region of the sky, and thereby, the direction of the Moon, under the conditions of the experiment shown in the last part of table 2.

It seems possible, therefore, that the orientation of talitrid amphipods to moonlight does not require a point source of light but can be based on the brightest general region of the total field of illumination. Such an ability might be particularly useful to these animals during night-time orientation on beaches where clouds and fog often partially obscure the position of the Moon.

If this interpretation is correct, then the inconsistent directions often noted during mirror experiments (fig. 2), as well as the shorter vector lengths, would be expected. A mirror experiment would involve exposing the animals to two possible orienting stimuli: skyglow from the real Moon, visible around

the edges of the screen; and a point source of light, largely without skyglow, from the mirror.

My own qualitative observations, as well as those of others (ref. 2)² suggest that talitrid amphipods are usually disoriented on moonless nights; but as shown in table 1, lack of orientation can also occur, for unknown reasons, on nights when the Moon is visible. Therefore, disorientation on moonless nights—unless it is observed in a very large number of cases—is weak evidence, at best, for the involvement of the Moon in the orientation. It has, in fact, recently been claimed that *Talitrus saltator* can orient significantly both during the daytime and at night, without seeing either the Sun or Moon (ref. 8). The implication of that article is that some unspecified geophysical directional cue, of a category not usually recognized as being biologically effective, was involved. Magnetism was apparently excluded.

It is my opinion that these claims are, at present, insufficiently substantiated to warrant serious concern about the results obtained in Moon-orientation experiments. The published description of experimental methods is extremely brief; it is, therefore, not clear that some accidental aspect of the ex-

TABLE 2.—Data of October 17, 1964

| Time | Lunar azimuth | Vector length | Orientation azimuth | Angle with Moon |
|-------|---------------------|---------------|---------------------|-----------------|
| 22:59 | 211° | 0.64 | 156° | -55 |
| 23:04 | 213° | 0.74 | 167° | -46 |
| 23:06 | ^a 33° | 0.89 | 296° | -79 |
| 23:07 | ^a 33° | 0.93 | 296° | -79 |
| 23:18 | ^b (216°) | 0.79 | 171° | -45 |
| 23:20 | ^b (217°) | 0.68 | 188° | -29 |

^a Azimuth of mirror from which lunar disk was reflected onto chamber.

^b Azimuth of Moon, which had been hidden by opaque screen since 23:06.

perimental arrangement—e.g. cloud pattern, or the light source used for photography, or the slope of the observation chamber (ref. 9) or wind direction (ref. 2)—did not sometimes provide directional stimuli. Beyond this, the statistical test used to assess the results is clearly inappropriate: multiple photographs of the animal positions were used to increase unjustifiably the statistical degrees of freedom, and no allowance was made for possible interaction between animals. Since the reported orientations were much more dispersed than those usually found when the animals see either the Sun or the Moon, concern about subtle artifacts in the experimental situation, as well as about appropriateness of statistical methods, are of extreme importance in evaluating a study of this sort.

While the claim of Van der Bercken et al. remains, in my view, unproven, the lack of complete success in the mirror experiments shown in figure 2 also leaves open the possibility of unknown influences in talitrid orientation. The Moon is clearly implicated as an important orienting stimulus by the fact that reflection of the Moon's image from a mirror produces large deviations from the prior orientation direction, deviations which usually are much greater than would be expected due to chance alone. Nevertheless, it remains possible that some other factor, such as the Earth's magnetic field, also jointly affects the net directions of orientation.

One form of this alternative hypothesis which I have considered and rejected is that the initial orientation is due primarily to magnetism (or a similar clue); that the animals thereafter note the direction of the Moon, and subsequently use the Moon as a reference stimulus. This admittedly rather complex hypothesis might account for the observed inconsistencies in the mirror experiments; the hypothesis predicts, however, that if the amphipods, on their first exposure in

the orientation chamber, see the Moon reflected from a mirror, their orientation should be in the same compass direction as that of animals which initially see the unreflected Moon. Subsequent exposure to the real Moon should then lead these experimental animals to orientation in the opposite direction. An experiment which contradicts this prediction is summarized in figure 3.

The net weight of the evidence, in my opinion, supports the assumption that moonlight is the primary and probably only significant orienting stimulus in the experiments which have been performed on Moon orientation. This is, however, probably the weakest link in the chain of evidence leading to the Moon-compass hypothesis. Should convincing evidence become available that talitrids orient consistently in a constant compass direction by means of some subtle non-visual stim-

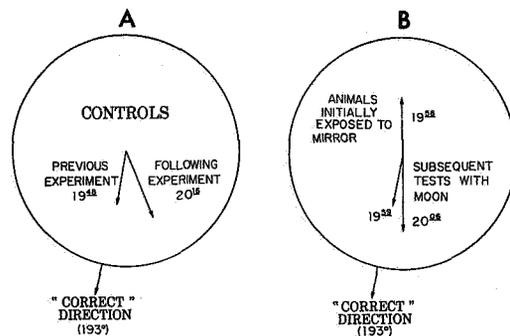


FIGURE 3. Test of hypothesis that initial orientation is based on non-visual stimuli. In these two graphs, north is upward; vector length scaled as in figure 1B. (A) Orientation directions assumed in preceding and following "standard" experiments, with Moon visible; (B) Orientation of animals initially exposed to lunar image reflected from mirror (upward arrow), and subsequent orientation of these same animals, when exposed to actual Moon (downward arrows). Results are compatible with the interpretation that the Moon's image is the only significant directional clue. From Malibu experiments, October 17, 1964.

ulus, then all description in terms of changes in orientation angle with changes in lunar azimuth could be misleading: an artificial but necessary consequence of non-visual orientation in a constant compass direction. Hence, it should be reemphasized that the assumption that moonlight—and nothing else—is responsible for the observed orientations underlies all subsequent discussion.

Question III

Are the directions assumed by talitrids ecologically appropriate, when they orient by moonlight?

It is generally accepted that celestial orientation as shown by talitrid amphipods in an orientation chamber reflects the capacity to return only to the strandline on the beach from which they were collected, and not necessarily to a particular point on the beach. Even an orientation which is within 60° of the "correct" direction would permit animals which had been displaced landward to return to the strandline by covering a distance only twice as great as that necessary by the most direct route; a deviation of 75° would imply a four-fold increase in distance travelled, so only orientation more than about 75° "wrong" would be ecologically useless or misleading.

The data from the various experimental series are summarized in figures 4 and 5, and it is evident that when significant orientation occurred, most experimental series involved performances which were consistently better than the minimum required for the behavior to be ecologically useful. Only in my Naples experiments (fig. 5C) and, to a lesser extent, my La Jolla experiments (fig. 5B), were an appreciable number of the observations in an ecologically "wrong" direction. Craig's observations, for which individual data are not yet available, also involved an apparently

faulty choice of directions. He studied animals from three beaches, which faced NNW, SE and SSE, and concluded that when significant orientation occurred (which was seldom—see table 1), "the amphipods generally oriented in the northeast sector, a direction of puzzling ecological significance." Since no breakdown of these observations by beach-of-origin was given, it is conceivable that a major fraction of the observed statistically significant orientations in this study were also within, say, 60° of the appropriate direction.

Within the framework of this question about ecological significance, it seems appropriate to consider briefly whether the usefulness of Moon orientation for the animals under field conditions represents an adequate explanation for its evolutionary origin. It is, of course, true that the Moon would be above the horizon at night no more than half of the month; and that, in coastal areas, nighttime clouds and fog are often common and intense enough that the animals would be unable to perceive or determine the Moon's direction even when it is above the horizon. One must presume, then, that orientation by the Moon is only a supplementary mechanism for direction finding by talitrids on the beach at night, and indeed, other mechanisms have been documented, including orientation to wind direction (ref. 2), and visual orientation to conspicuous topographic features (ref. 10).

Granted that the amphipods may seldom in nature have both the need and the opportunity to use the Moon as a basis for orientation, it nonetheless seems plausible that, at least occasionally, for some individuals in the population, the capacity may have a major influence on survival. The persistence, through evolution, of a given behavioral pattern does not require that the behavior regularly be used by all members of the population, nor even that the behavior be used oc-

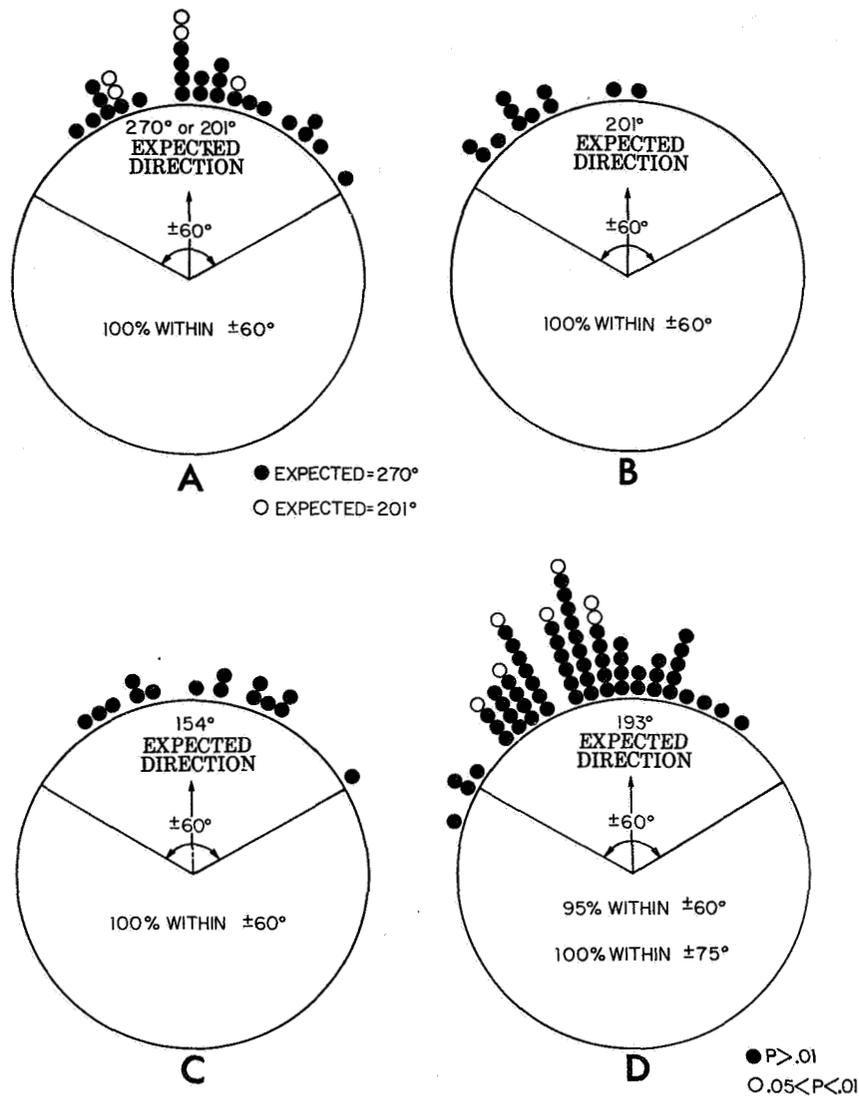


FIGURE 4. Best results for ecological appropriateness of lunar orientation. "Correct" direction (i.e. toward sea on beach of origin) is upward in these graphs as well as in figure 5. Each small circle represents results from a separate experiment; solid circles represent results statistically significant (with reservations—see footnote 3 in text) at the 0.01 level; open circles, at the 0.05 level. (A) Data from ref. 3; (B) Data from ref. 5; (C) Data from ref. 6; (D) Data from Malibu experiments (Appendix 2).

asionally by each individual. Even occasional use of the capacity by a fraction of the population would be sufficient to maintain

the appropriate genes in the population, provided that the survival value of the behavior, when utilized, were sufficiently great. It

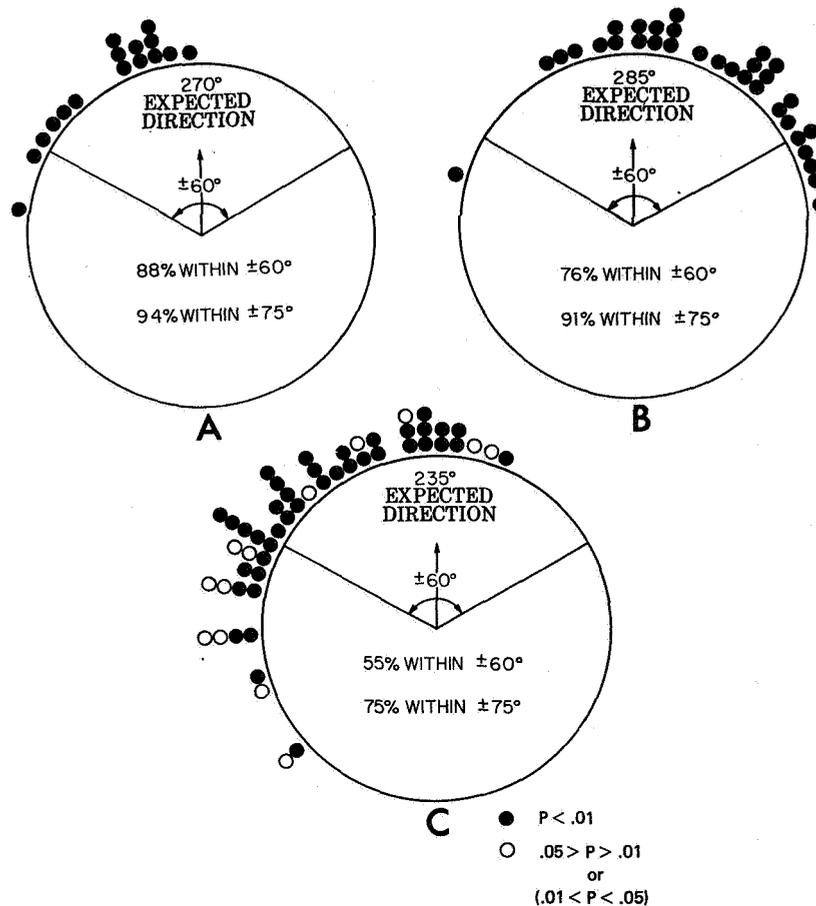


FIGURE 5. Less convincing results for ecological appropriateness of lunar orientation. Symbols as in figure 4. (A) Data from ref. 2; (B) Data from ref. 4; (C) Data from Naples experiments (Appendix 1).

would be an oversimplification of evolutionary processes to argue against the plausibility of Moon-compass orientation only because it would not always be adequate to meet the needs of the animals.

Question IV

Does the lunar orientation of talitrid amphipods involve the capacity to orient in a "correct" direction, regardless of the position of the Moon?

This question is of particular interest for

the physiologist concerned with a mechanism; it embodies the essence of what would normally be understood as Moon-compass orientation: the process of time-compensation for lunar movement. Except in the tropics, the amphipods could, in principle, orient to within about 90° of the ecologically correct direction, by means of a non-compensatory, fixed angle of orientation to the Moon, provided that the fixed angle chosen were correlated with the orientation of the home beach. The results shown in figures 4 and 5 could

conceivably all be due to such a non-compensatory orientation.

Contrary to my previous interpretation (ref. 4), it is now my opinion that the question of time-compensation in talitrid orientation must be answered with a qualified affirmative. The qualifications are the following: one must accept the assumption that the Moon is the only orientational stimulus leading to the performance (See Question II, above.); and one must grant that, for reasons as yet undetermined, the animals sometimes fail to show their full orientational capacity. Talitrids are sometimes able to compensate in their orientation for changes in the direction of the Moon, but they do not always do so.

Consideration will be given in a later section to the various factors, including duration of captivity and lunar phase, which do or may influence the performance of talitrids in their Moon orientation. Initially, however, let us ignore such factors and look at the overall results to see whether the amphipods show orientation which varies with position of the Moon. The data are summarized in graphical form in figures 6 and 7. The experiments covered in Figure 6A should be regarded with caution, since it is uncertain which of the results are, as single experiments, statistically significant. In all other cases, the results included in the graphs involved orientation which was statistically significant at the 0.01 level (solid circles), or the 0.05 level (open circles; see footnote 3).

In nearly all experimental series, there are major deviations of the observations from expectations, as is implied, also, in figures 4 and 5. Nevertheless, there is, in each experimental series, a trend toward a smaller angle of orientation as the Moon moves from east through south to west (i.e. lunar azimuth increases). In the results shown in figure 6, the slopes of the regression lines are not significantly different from the expected value of

—1.0. In the experimental series included in figure 7, the slopes of the calculated regression lines are significantly different from zero, indicating some compensation; but the slopes are also significantly different from —1.0, indicating that compensation was not always as complete as expected.

An overall view of the data thus demonstrates that the orientation of talitrids to the Moon is not a fixed-angle orientation, but involves time-compensation, which seems in some cases quite complete (figure 6), and in other cases (figure 7) only partial: qualitatively correct but quantitatively insufficient. Even in my Naples experiments, in which the directions of orientation were poorest in terms of beach-of-origin (fig. 5C), the amphipods were, in a significant fraction of the experiments, changing their orientation in an ecologically appropriate direction with changes in lunar azimuth (fig. 7C).

Question V

What is the evidence, based on experiments performed within a single night, that the amphipods change their orientation, relative to the Moon, in the appropriate direction?

True Moon-compass orientation should involve two phenomena: compensation for changes in lunar position during each night, and compensation between nights for changes in lunar position with changes in lunar phase. The mechanism might be the same, but that remains only hypothesis; different kinds of evidence must be examined to determine whether the two phenomena are demonstrable, and both kinds of evidence are intermingled in the graphs of figures 6 and 7.

The data which show the clearest evidence for appropriate compensation within single nights are summarized in figures 8 and 9, and include four nights of data from the

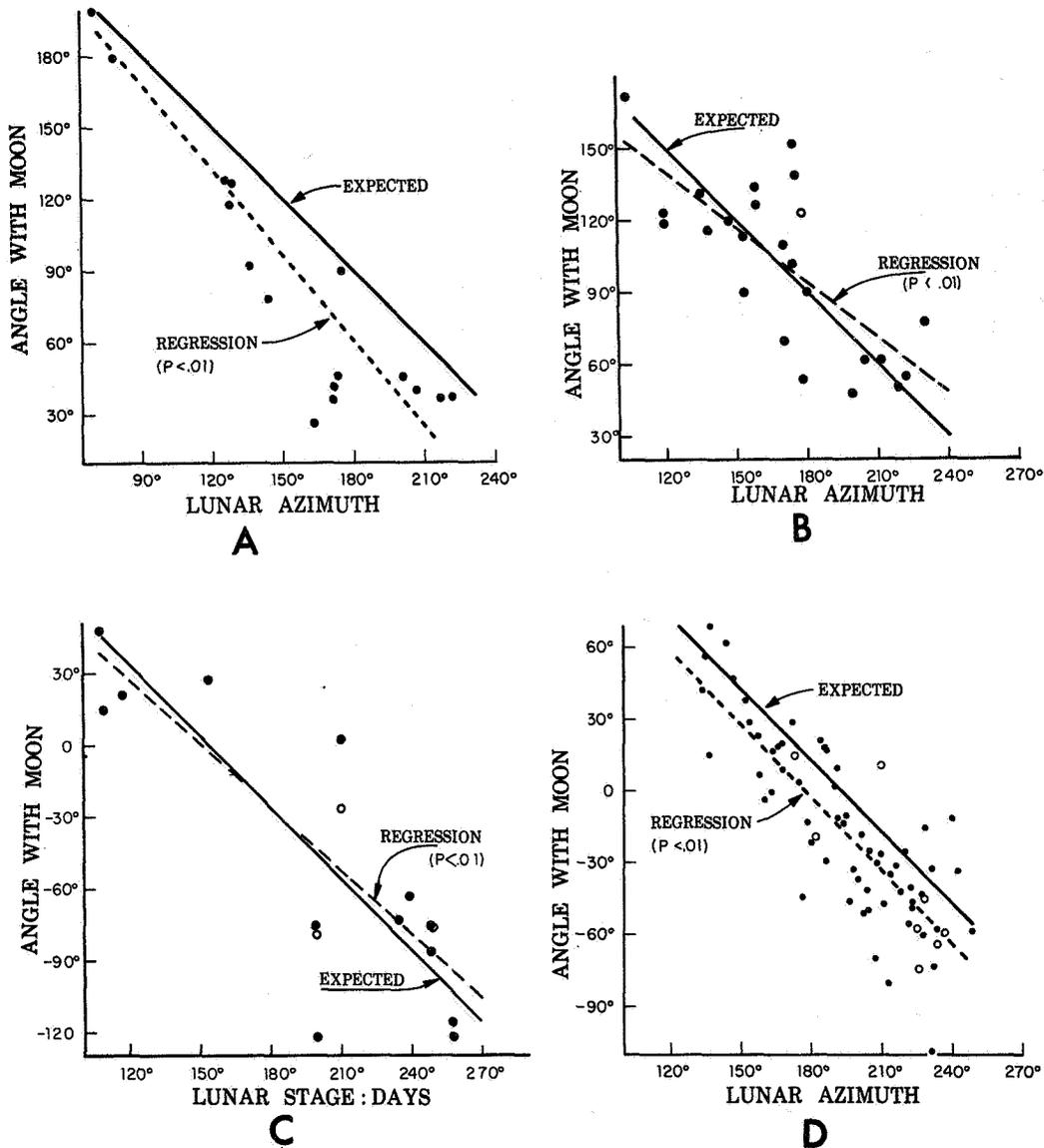


FIGURE 6. Best results showing variation in orientation angle with changes in lunar azimuth. Lunar azimuth measured clockwise from north; orientation angle measured with clockwise being positive. Algebraic sum of lunar azimuth and orientation angle is, therefore, azimuth of orientation, and expected relationship has slope of -1.0 . Except in figure 6A, solid circles represent orientation significant (with reservations; see footnote 3 in text) at the 0.01 level, open circles at the 0.05 level. The calculated least-squares regression lines all have slopes which are significantly different from zero ($p < 0.01$) and slopes which are not significantly different from -1.0 ($p > 0.10$). (A) Data from ref. 2; (B) Data from ref. 3; (C) Data from ref. 6; (D) Data from Malibu experiments (Appendix 2).

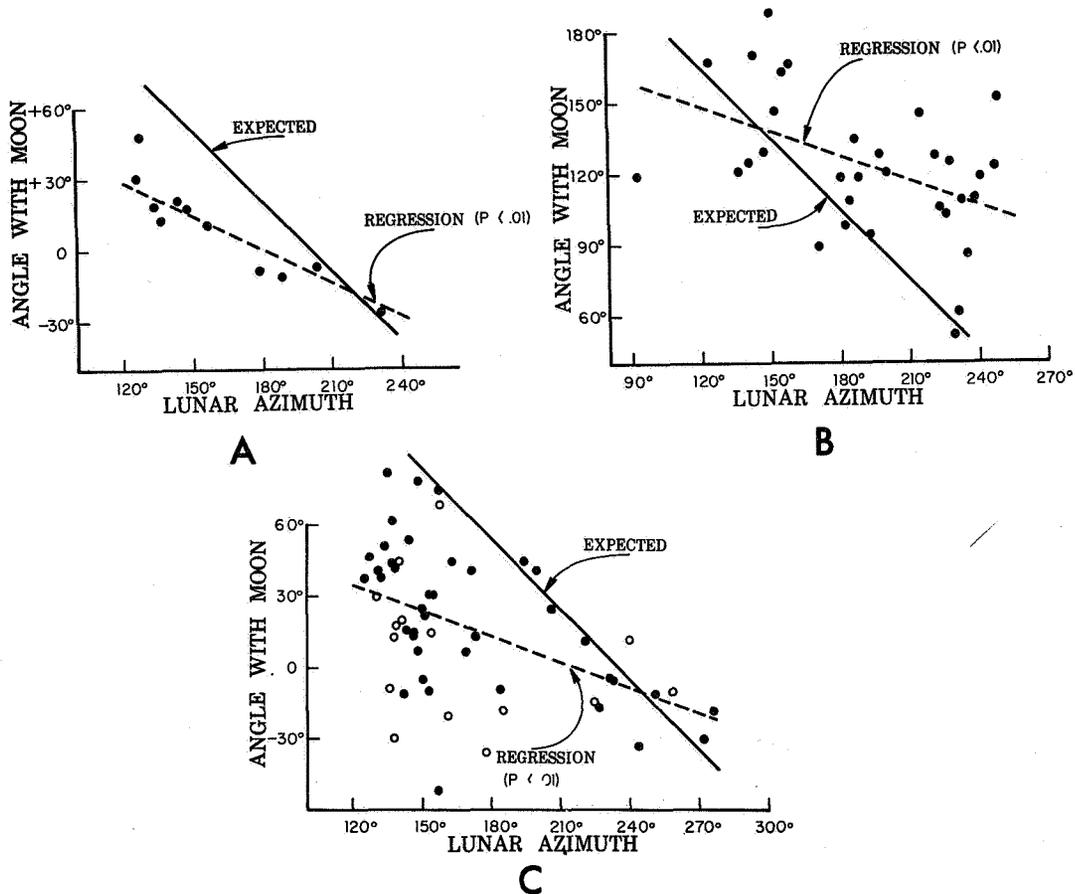


FIGURE 7. Poorer results showing variation in orientation angle with changes in lunar azimuth. Calculated regression lines all have slopes which are significantly different from zero ($p < 0.01$), but that are also significantly different from the expected value of -1.0 . See figure 6 for all other details. (A) Data from ref. 5; (B) Data from ref. 4; (C) Data from Naples experiments (Appendix 1).

Mogadiscio experiments, with two to six observations per night (fig. 8A); one night of data from the La Jolla experiments, in which at least two of the treatments ("natural light" and "redarkened", fig. 8B) produced significant trends; and three nights of data from my Malibu experiments (fig. 9A, B and C). In these latter data, the changes in orientation angle are so unmistakable that it would be superfluous to perform a statistical

test. It is perhaps surprising, but probably only a coincidence, that the best data for time-compensation within single nights include no data from *Talitrus saltator*, the species which has been most extensively studied for Moon orientation.

Somewhat less convincing data are summarized in figure 10; four nights, with no more than four observations per night, from the Castiglione experiments with *T. saltator*,

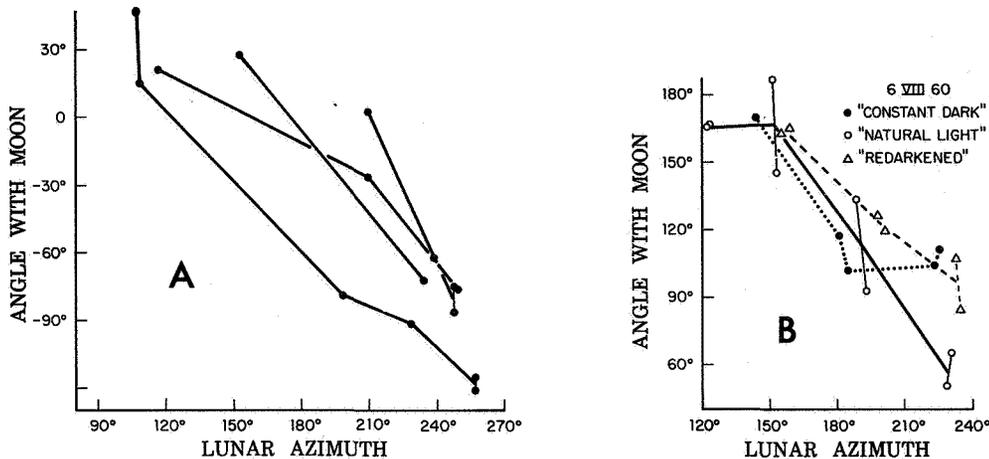


FIGURE 8. Good results showing compensation for changes in lunar azimuth within sets of experiments conducted during single nights. Symbols as in figure 6. (A) Data for 4 nights from ref. 6; data for different nights connected by separate lines. (B) Data for one night, with three different treatments of animals; see ref. 4, for details of treatment.

(fig. 10A), in which trends toward decreasing angle seem evident, but with slopes decidedly less than -1.0 ; and data from three nights in my Naples experiments, again with *T. saltator* (fig. 10B, C and D), in which there was such large scatter between experiments that none of the calculated regression lines is significantly different from zero at the 0.01 level.

Data from two additional nights of my Naples experiments are presented in figure 11A, and data from two nights from my La Jolla experiments are presented in figure 11B. In these cases, there was no evidence whatever for consistent changes in orientation angle during the night although changes of up to 85° should have been expected. Figure 11C, which is based on eight sets of experiments with *T. saltator* in the San Rossore II series, indicates that in these experiments, also, there was no consistent trend for the animals to compensate within single nights. Finally no evidence for or against compensation within single nights can be derived from

the San Rossore I experiments. Within a single night, the largest change of lunar azimuth between observations was 10° , so the expected changes in orientation angle are too small to be detectable.

In summary of these data, then, the evidence is unequivocal that talitrid amphipods have, in some experimental series, shown changes in orientation angle relative to the Moon during a single night, even when maintained in complete darkness prior to observation. These changes involve approximately appropriate compensation for changes in lunar azimuth. In my opinion, however, the evidence is equally clear that the animals do not always show this capacity (fig. 11A, B and C). The reasons for these failures are at present unknown, but various possible experimental complications will be considered in a subsequent section.

Question VI

Are the amphipods able to compensate in their orientation for day of the lunar month?

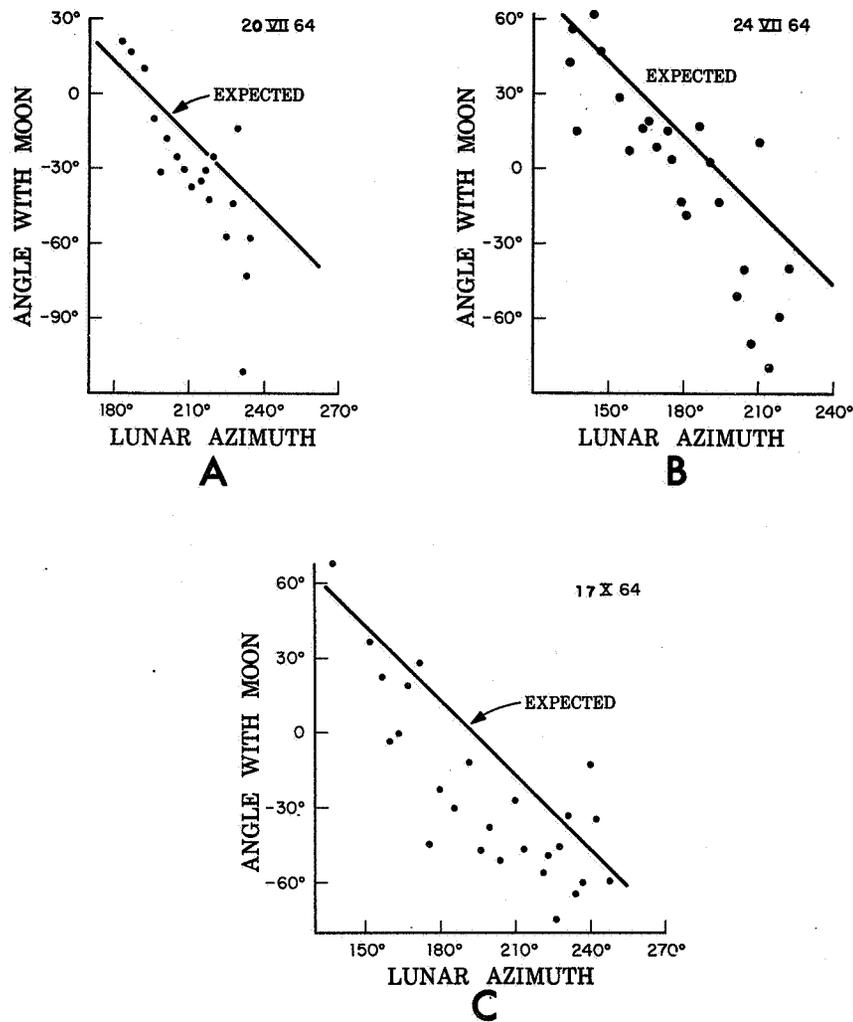


FIGURE 9. Good results showing compensation for changes in lunar azimuth within experiments from single nights. Symbols as in figure 6. Data from Malibu experiments (Appendix 2). (A) July 22, 1964; (B) July 24, 1964; (C) October 17, 1964.

This question involves a critical property by which Moon orientation differs from Sun orientation; because the Moon rises about 50 min later each night, the appropriate angle of orientation, relative to the Moon, changes not only from hour to hour but, for a given hour, changes from night to night. It is conceivable that the amphipods might use some

variant of the 24-hr endogenous rhythmicity, which is presumably responsible for Sun-compass orientation, in order to accomplish changes in orientation angle during the night; the "successful results" of figures 8 and 9 could easily be described by a change in angle of 15° per hour such as is implicit in Sun orientation. Such a mechanism could not

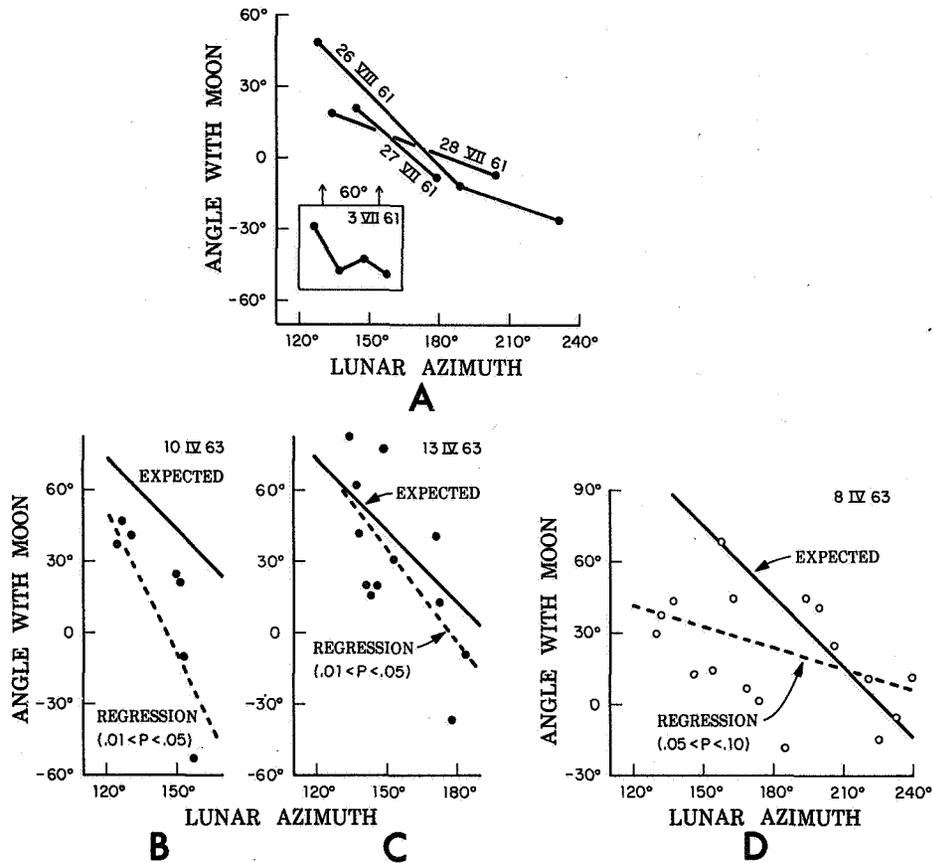


FIGURE 10. Less convincing results, suggesting some compensation for changes in lunar azimuth within experiments from single nights. Symbols as in figure 6. (A) Data from ref. 5; the trend toward negative slope does not seem to approach the expected value of -1.0 ; (B), (C) and (D): Data from Naples experiments (Appendix 1). None of calculated regression lines has a slope significantly different at 0.01 level from zero, although trends toward negative slope are evident.

account, however, for changes in orientation angle from night to night.

The question posed can best be answered by examining whether the angle of orientation for a given time of night varies with phase of the Moon. Such an analysis requires observations made at comparable times of night, on nights of a different stage in the lunar cycle, a requirement which greatly restricts the usable data. My Malibu experi-

ments involved only two phases of the Moon, which differed by only 4 days, so the difference in orientation angle, for any time of night, is only about 50° . Nevertheless, these data provide striking evidence (fig. 12) for differences in orientation angle at comparable times of night. There is some slight overlap in the observations at different lunar phase, but it seems unnecessary to perform statistical tests to convince even the skeptic that the differ-

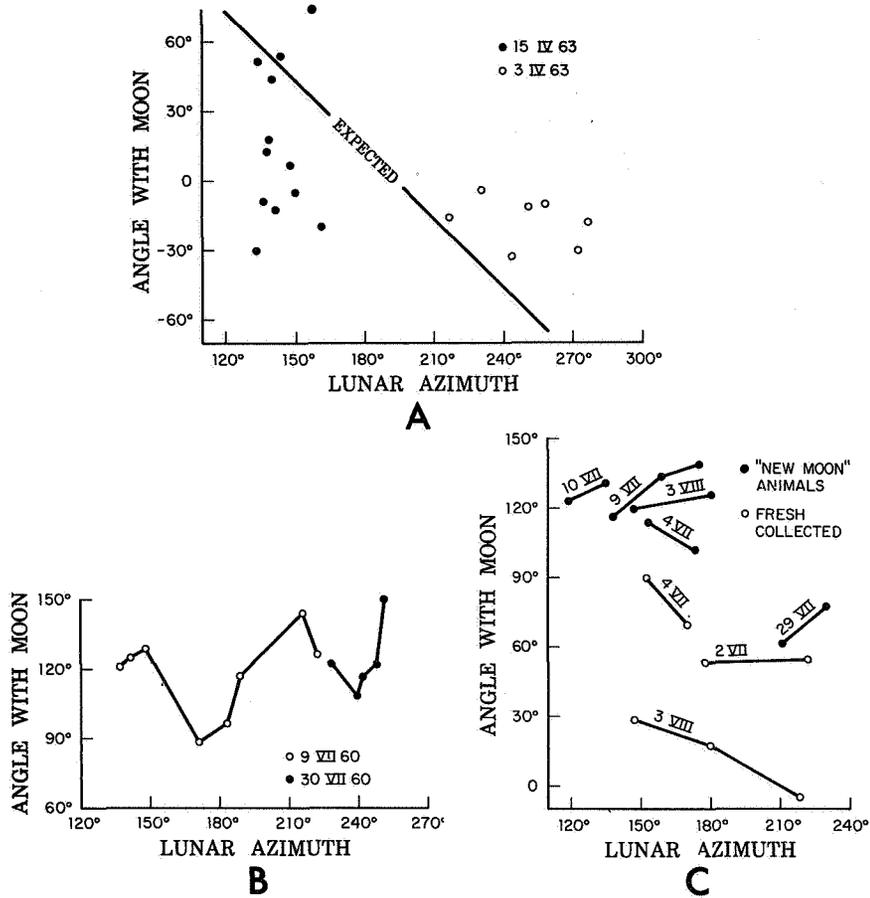


FIGURE 11. Results showing no consistent compensation for changes in lunar azimuth from experiments during single nights. Symbols as in figure 6. (A) Data from two nights of Naples experiments (Appendix 1); (B) Data from two nights, from La Jolla experiments, ref. 4; (C) data from ref. 3.

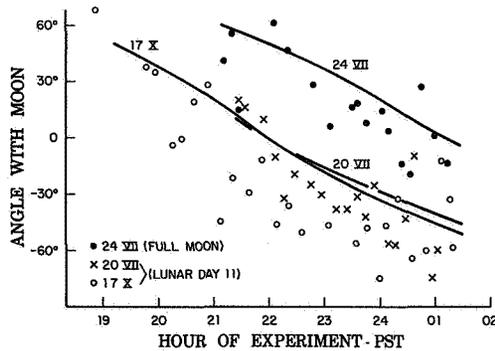


FIGURE 12. Orientation angle as a function of time of night, for different lunar phases: Malibu data (Appendix 2). July 20 and October 17 data for lunar day 10; July 24 data for lunar day 14 (full Moon). Lines represent "expected" orientation on the respective nights. Note that observations on July 24 involve larger angles with the Moon at comparable times of night.

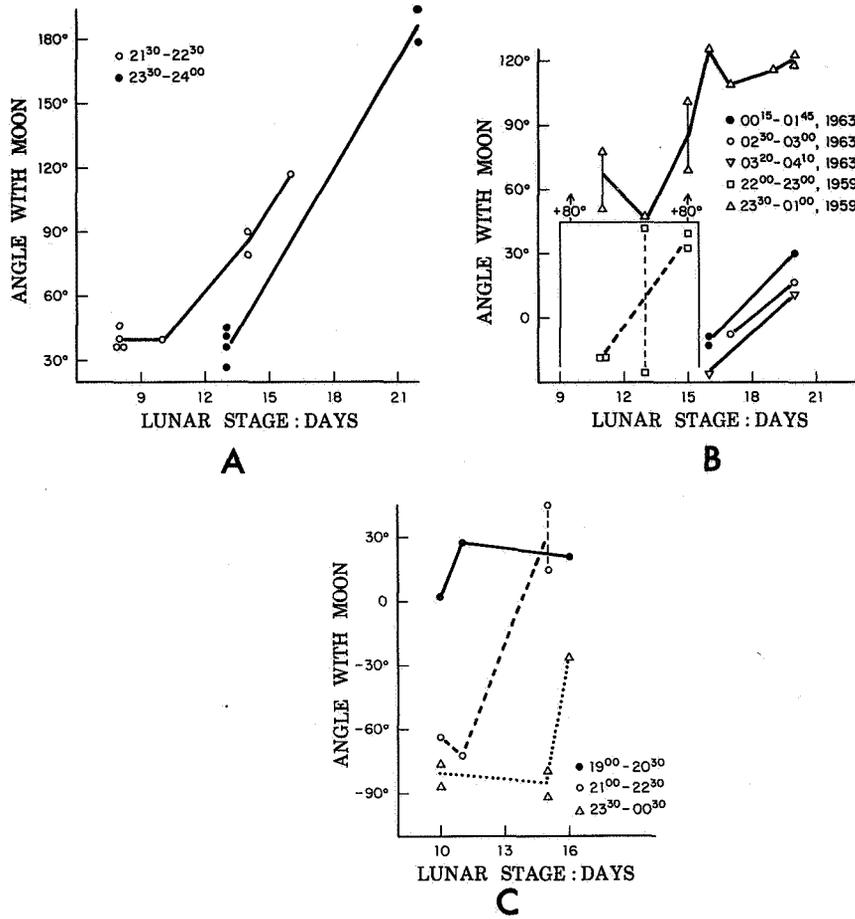


FIGURE 13. Orientation angle as a function of lunar phase, for different times of night. "Correct" compensation should involve an increase in angle of about 12° per day, on the average. (A) Data from ref. 2; (B) Data from ref. 3 and ref. 5; (C) Data from ref. 6.

ence of 4 days in lunar phase was correlated with consistent hourly differences in orientation angle relative to the Moon.

Another type of graph is presented in figures 13 and 14: the data have been grouped according to time of night, and the angle of orientation is plotted against lunar phase. Figure 13 includes data from three studies of *Talitrus saltator* (fig. 13A and B) and one study of *Talorchestia martensii* (fig. 13C); Figure 14 is based on the data from my Na-

ples experiments, also with *Talitrus saltator*. On the average, the expected change in orientation angle in these graphs should be an increase of about 12° per day.

The data clearly show trends in the appropriate direction, some of which are convincing, others less so: for a given time of night, the orientation angle was usually greater during the latter part of the lunar cycle, although the scatter was often very large. Again, even my Naples experiments,

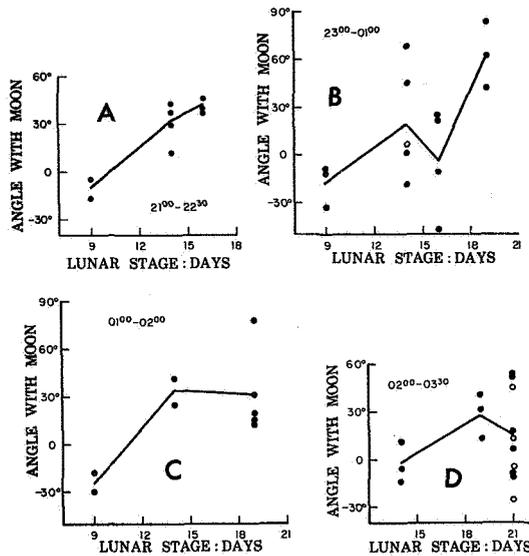


FIGURE 14. Orientation angle as a function of lunar phase, for different times of night. Data from Naples experiments (Appendix 1).

which, on the basis of ecological considerations might be considered largely "unsuccessful" (fig. 5C), showed relatively consistent evidence for conformity to this expected trend (fig. 14).

At the very least, a simple daily rhythm seems completely inadequate to account for the data as presented in figures 12, 13, and 14. The amphipods seem able to compensate to some extent for changes in day of the lunar cycle.

Question VII

What experimental factors might account for some of the variability in the Moon orientation of the amphipods?

A very serious problem for the interpretation of data on Moon orientation of talitrids is that the performances of the animals are so often inconsistent with or contradictory to the Moon-compass hypothesis. It is my opin-

ion that the sources of this variability are at present largely unknown, although some possible sources deserve detailed consideration.

In a criticism of my La Jolla experiments (especially those of fig. 11B), Papi and Pardi (ref. 5) attempt to explain the poor performance by emphasizing the fact that I did not heat and dehydrate the air in the observation chamber. It is their contention (refs. 2 and 5) that when talitrids are placed in an orientation chamber at night, the animals initially show a simple positive phototaxis, orienting directly toward the Moon, and only gradually thereafter, during some several minutes, assume the correct direction of orientation, at some angle to the lunar position. It is claimed that the heating or dehydration of the chamber provides the "releasing stimulus" for reorientation away from positive phototaxis.

The initial observations of Moon orientation of talitrids (ref. 2) purportedly required dehydration of the air in the chamber; the documentation for this claim consists of one example (*ibid.*, fig. 7) which is somewhat unconvincing; the initial orientation was purportedly complicated by skyglow from city lights. In a subsequent paper, Papi and Pardi (ref. 3) stated that dehydration of the air is unnecessary, but asserted (without supporting data) that heating the chamber is desirable, a procedure which they substituted for dehydration in all subsequent experiments. It should be noted, however, that some relatively successful experimental observations have been made without either drying or heating the observation chamber artificially (fig. 8B), and some experiments in which the observations depart very markedly from "expectations" were made in a chamber in which the air was both heated and dehydrated (Naples experiments, fig. 10B, C and D; and fig. 11A) or at least heated to 20°C (data of Craig); footnote 2.

My own data lend very little support to the interpretation of Papi and Pardi; neither the initial positive phototaxis, nor consistently more correct reorientation after exposure to "releasing stimuli" can be well documented in the data. In the La Jolla experiments, the published data are based on animals which were photographed during their first minute in the orientation chamber which was neither heated nor dehydrated. Both on nights of "poor" performance and of "good" performance, the initial angle of orientation averaged about 120° , a radical departure from positive phototaxis. The smallest observed angle of orientation, relative to the Moon, was more than 50° away from positive phototaxis.

In my Naples and Malibu experiments, the amphipods were removed from their darkened containers, rapidly placed in the orientation chamber (which was heated and contained CaCl_2 to dehydrate the air) and their positions were then photographed within one minute of their initial exposure to

moonlight. The animals were then left undisturbed for 5 min, and a second photograph was taken. The difference between initial orientation and that after 5 min showed an overall trend toward greater angles with the Moon after 5 min, such as might be expected if the animals were becoming less positively phototactic. The differences were, however, usually very small (table 3), and may represent an effect of the photographic lighting which accompanied the first photographs, such as is discussed below under the consideration of multiple photoflashes. Furthermore, the initial orientations were generally consistently different from simple positive phototaxis. The animals tended to orient initially at some angle with the Moon, an angle which then, more often than not, tended to become slightly larger.

In terms of ecological considerations, it also seems surprising, to say the least, that heating to temperatures greater than 20°C and/or dehydration of the atmosphere would

TABLE 3.—Changes in Orientation During 5 Minutes in Chamber

| Experimental series | Date | Number of cases with: | | Median change ^a (deg) |
|---------------------|------------------|----------------------------|----------------------------|-------------------------------------|
| | | Greater angle ^a | Smaller angle ^a | |
| Malibu..... | July 20-21..... | 15 | 4 | +5 |
| | July 24-25..... | 8 | 12 | -4 |
| | Oct. 17-18..... | 17 | 8 | +6 |
| | Total..... | 40 | 24 | |
| Naples..... | April 3-4..... | 3 | 4 | -1 |
| | April 8-9..... | 6 | 7 | -4 |
| | April 10-11..... | 5 | 2 | +3 |
| | April 13-14..... | 10 | 3 | +16 |
| | April 15-16..... | 8 | 4 | +2 |
| | Total..... | 32 | 20 | |
| Grand Total..... | | 72 | 44 | |

^a Numbers of cases and angle values in this table are based on the difference between the absolute value of the initial angle with the Moon and the absolute value of the final angle.

be necessary for talitrids to use lunar orientation correctly. Air temperatures greater than 20° C are very seldom encountered at night on temperate-latitude beaches; in many areas where the animals are found, such nocturnal temperatures never occur. Furthermore, the air near the sea is usually nearly saturated with humidity at night.

The contention, then, that either low humidity or an air temperature of at least 20° C is necessary for talitrids to use their Moon-compass orientation seems to imply that the capacity would be largely an experimental artifact: demonstrable only in an orientation chamber which has been artificially heated or dehydrated, but essentially useless to the animals on the beach. This I find difficult to accept on evolutionary grounds.

It may, indeed, be true that talitrids, under some circumstances, initially orient toward the Moon with a positive phototaxis, and thereafter, given certain "releasing" stimuli, will orient in the ecologically correct direction. If so, the contention is poorly documented in the published literature and is unsupported by my own experimental observations; the phenomenon, therefore, should not be considered common, nor invoked as a general explanation for the inconsistencies in the available data.

Since all published experiments of the Italian workers involve orientation of animals which had been 5 min or longer in the orientation chamber, I have used the data from second photographs (taken after 5 min) in graphs of the Naples and Malibu experiments, but data from the initial photographs would not appreciably alter any of the graphs or conclusions. It is probably also advisable to heat and dehydrate the observation chamber in future experiments with lunar orientation of talitrids, but the argument in favor of this procedure must be based on consistent meth-

odology, and not on any demonstration that it will affect the results.

I have proposed (ref. 4) that time-compensation for changes in lunar azimuth may require that the animals experience sunset and/or moonrise on the night of the experiment, but an appreciable body of subsequent data (including my own data in Appendixes 1 and 2) now contradicts that interpretation, which was proposed initially to account for the differences between the data of figures 8B and 11B. The data of figure 8B demonstrate that the prior light regime can modify the orientational performance, but the contention that sunset and moonrise on the night of the experiment are, of themselves, the critical factors in the time-compensation process is no longer tenable. Differences in the performances of the animals in different experimental series cannot, in general, be attributed to this factor.

The experiments of the Italian workers with Moon orientation have usually involved taking a sequence of ten or more photographs of the animals, at intervals of a minute or two, using photoflash. The possibility exists that such a series of light flashes might affect the performance of the animals, and I have published suggestive evidence that this is the case (ref. 4): in two experiments, with ten photographs each, taken within 15 min, the animals significantly decreased their angle of orientation relative to the Moon, from first to last photograph; in one case, by 68°, in the other, by 48°. In a similar set of observations, as part of the Malibu experiments, the animals also decreased their angle of orientation relative to the Moon from the first to the tenth photograph in five cases out of six, with a median decrease of 33°. In another similar series of experiments with *Talitrus saltator* (ref. 5), the animals also decreased their angle of orientation relative to the Moon,

from the first to the last photograph, in nine cases out of 11 (i.e. the animals became more photopositive toward the Moon, although Papi and Pardi apparently did not recognize this trend in their data). In this latter study, however, the changes were all small, with a median decrease of only 7° . Differences in experimental methods may well be responsible for the fact that Papi and Pardi recorded much smaller changes than I. Their procedure of photographing the animals from beneath rather than from above would be expected to reduce greatly the intensity of the light which the animals experience from the photoflash.

In my opinion, it still seems desirable, as I have previously suggested (ref. 4), to make only a minimum number of photographs of the animals' positions, with each group of animals, when using photoflash; this precaution seems particularly important when photoflash is given from above. It should be borne in mind that the additional data obtainable from multiple photographs do not add appreciably to the statistical reliability of the data, since, in my opinion, degrees of freedom should be based on observations from different animals. The performance of the species under a given treatment can be far better evaluated by single photographs of separate groups of amphipods, similarly treated, than by multiple photographs of the same, single group—even if the photoflash were to have a negligible influence. This methodological problem, however, is unlikely to account for a major portion of the inconsistencies in the orientational performances evident in the data discussed here. My own data, which include both good and poor performances, are not based on such series of multiple photographs.

Many of the available data lend support to the interpretation that there is greater in-

ternal consistency in the orientations observed of a group of animals at times of full Moon than at first and last quarters of the Moon. The vector length, (which is inversely related to the degree of scatter within an experiment) shows an overall consistent trend toward greater values at full Moon than at other lunar phases. Highly significant differences can be demonstrated in several of the data series (table 4). This trend is, of course, not surprising, since the full Moon provides a much brighter stimulus object than does the Moon at first and last quarters. The trend lends further, indirect support to the conclusion drawn to Question II above, that the Moon is the major factor responsible for nighttime orientation. The lesser scatter of directional choices within an experiment would mean that the average direction observed of the orientation of a group of animals is likely to be more reliably estimated at times of full Moon, but this consideration, also, seems unable to account for a major portion of the inconsistencies in the data available.

On the assumption that the orientation is, indeed, based on position of the Moon, one must also presume that compensation for changes in lunar azimuth is based, in some manner, on an internal physiological timing process. It is, then, to be expected that presumably free-running "internal clocks" should, on the average, show a trend toward deviation from correct orientation when the animals have been kept for longer intervals (in some cases, more than 2 weeks) in the laboratory. There is certainly a consistent trend for the amphipods to be less well oriented (i.e. shorter vectors are observed, implying greater scatter within the group) when the animals have been maintained for several days in the laboratory under constant conditions (see table 1). These decreases ob-

TABLE 4.—*Dependence of Vector Length on Lunar Stage*^a

| Experimental series | Lunar stage (days) | Average vector | Number of experiments | Probability of no difference |
|---------------------|--------------------|----------------|-----------------------|------------------------------|
| San Rossore I..... | 13, 15, 16 | 0.79 | 8 | $p < .05$, <i>t</i> test |
| | 11, 17, 19, 20 | 0.62 | 9 | |
| La Jolla..... | 15, 16 | 0.66 | 24 | $p < .01$, <i>t</i> test |
| | 8, 22 | 0.53 | 13 | |
| Naples..... | 9 | 0.59 | 8 | $p < .001$, <i>F</i> test |
| | 16 | 0.71 | 3 | |
| | 19 | 0.68 | 7 | |
| | 21 | 0.42 | 7 | |
| Santa Barbara..... | 14, 15, 16 | 0.39 | 32 | $p < .001$, <i>t</i> test |
| | 7, 8, 9, 10 | 0.29 | 27 | |

^a All data are for freshly collected amphipods.

served in vector length would, of course, be expected on the basis of desynchronization of the free-running rhythms of the various individuals within the population.

A question of broader interest, however, is whether there is a consistent trend in the directions chosen following longer laboratory holding of the animals, and it must be admitted that no such trend is evident. The overall impression conveyed by the data is that the average rate of the timing process differs very little from the appropriate value of about 14.5° per hr. This conclusion should, however, be examined in more detail.

Very good performances involving time compensation have often been observed of animals which were collected sometime within the day preceding the experiment (ref. 2; tables 1 and 2 of ref. 3; table 2 of ref. 4; ref. 6; and the July data from my Malibu experiments), although there are some exceptions (table 1 of ref. 4; and parts of my Naples experiments). See Appendix 1. Good orientation was also observed in the Malibu experiments, on October 17 and 18, of animals kept for 2 and 3 days in complete darkness. The only extensive series of "successful" experiments in which the animals had

been kept undisturbed in the laboratory for longer than 3 days are the data in table 3 of ref. 3, the relevant parts of which are reproduced here as table 5.

It appears that the simplest interpretation of the data for the animals collected in June is that they oriented with an essentially constant angle toward the Moon; there is no appreciable correlation between observation and expectation ($p > 0.50$). Thus, the only data which lend some support to the hypothesis, that talitrids can orient with compensation for changes in the direction of the Moon after prolonged maintenance in constant darkness, are the data from the animals collected in July (four observations shown in the lower part of table 5) only two of which differ appreciably from those of the animals collected in June.

It is my opinion, then, that insufficient data are available to draw conclusions about the long-term precision of the biological timing processes which underlie Moon-compass orientation. Good evidence for the continuous operation of the timing process for 2 to 3 days is available, which can sometimes permit the animals to compensate correctly (\pm about 30°) for changes in lunar azimuth (Malibu

TABLE 5.—*Orientation of Amphipods Collected at Preceding New Moon*^a

| Date of experiment | Days since | Angle expected | Angle observed |
|---------------------------|------------|----------------|----------------|
| Animals Collected June 19 | | | |
| July 2..... | 13 | 92° | 123° |
| July 4..... | 15 | 117° | 114° |
| July 4..... | 15 | 96° | 102° |
| July 9..... | 19 | 132° | 116° |
| July 9..... | 19 | 112° | 134° |
| July 9..... | 19 | 95° | 139° |
| July 10..... | 20 | 151° | 123° |
| July 10..... | 20 | 135° | 131° |
| Animals collected July 18 | | | |
| July 29..... | 11 | 59° | 62° |
| July 30..... | 11 | 40° | 78° |
| Aug 3..... | 15 | 123° | 120° |
| Aug 4..... | 16 | 90° | 126° |

^a Data from ref. 3.

data); and the animals are often not completely disoriented, after 2 to 3 weeks under constant conditions (table 5, and parts of table 1 from ref. 4), but these latter data do not necessarily implicate internal timing processes. A constant-angle of orientation, relative to the Moon, will describe nearly all these data.

CONCLUSION: A WORKING HYPOTHESIS

Because so many contradictions are evident in a comparison of the various experimental series, it seems safe to say that no simple explanation can account for all of the data on Moon orientation of talitrids. I would, nevertheless, in concluding this review, like to propose an hypothesis which is compatible with several of the more interesting aspects of the data. This hypothesis is, in fact, only a minor variant of the Moon-com-

pass hypothesis of Papi and Pardi, and I cannot present the hypothesis with the enthusiastic advocacy of a firm believer. My position is, instead, that this is an unattractive hypothesis which I offer provisionally, in the lack of any better alternatives but with the hope that it will eventually be disproven.

The hypothesis consists of three propositions:

(1) Observed cases of compensation for changes in direction of the Moon are based on an internal physiological rhythm with a period of about 25 hours which can persist for at least several days under constant conditions (also the proposal of Papi and Pardi, refs. 3 and 5).

(2) The zeitgeber for this rhythm may be either Moonlight or some factor associated with the tides (probably the former, in view of the recorded changes in the orientation due to treatments with light), but, in any case, the zeitgeber is not as compelling an

entraining agent as the daily cycle, so that even freshly collected animals, under some field conditions, may not have recently experienced synchronizing stimuli.

(3) If talitrids have been long removed from environmental entrainment, either artificially or naturally, the internal rhythmicity no longer exerts appreciable influence on the angle of lunar orientation; the system deteriorates into constant-angle orientation, with an angle which is determined by the beach of origin, but may be modifiable by lighting conditions.

At least four alternatives to this hypothesis have been proposed:

(1) Van den Becken et al. (ref. 8) have suggested that the amphipods do not, in fact, necessarily rely on the Moon for nocturnal orientation, but instead rely upon some other geophysical directional clue. As discussed previously, this hypothesis seems to me to lack adequate supporting data.

(2) I have previously suggested (ref. 4) that the amphipods might utilize a single-cycle time-compensation process initiated by the stimulus of moonrise. As discussed above, the evidence against this proposal is now overwhelming.

(3) Hoffmann (ref. 11) has suggested that the amphipods might utilize their Sun-compass orientation at night, with corrections applied on the basis of the shape of the lunar disc. The fact that successful mirror experiments have been performed both before and after full Moon (fig. 1A), as well as the fact that good orientation has been observed during a partial eclipse of the Moon (ref. 2), seem to argue against this hypothesis, as does the required visual acuity.

(4) Horridge (ref. 12) has proposed that the animals could utilize their Sun-compass with corrections based on the rate of change of lunar altitude. This hypothesis is apparently contradicted by the fact that in success-

ful mirror experiments, the altitude of the mirror, whether 30° or 60°, had no evident influence on the results (fig. 1A). Furthermore, this hypothesis, as proposed, is even less esthetically pleasing to me than the Moon-compass hypothesis. Even granted the sensory capacity of the animals to recognize, within a few seconds time, the rate of change of lunar azimuth and altitude, the application of a correction based on this information seems to me to be an extremely complicated process.

In my opinion, then, the data on lunar orientation of talitrids which require an explanation (especially fig. 4 and 5) can best be accounted for by the Moon-compass hypothesis, with the modifications proposed above—this, in spite of the fact that the assumption of two independent clocks makes the hypothesis basically unattractive to me.

SUMMARY

(1) Talitrid amphipods, when deprived of all obvious orienting stimuli except a view of the Moon and stars, usually (but not always) show non-random orientations which are internally consistent between replicate experiments.

(2) Reflection of the image of the Moon from a mirror onto the amphipods usually produces major deviations in their directions of orientation, indicating that lunar position is the main, and probably the only significant orienting stimulus in these experiments.

(3) When non-random orientation is observed, the directions of orientation are usually, but not always, ecologically appropriate, that is, in a compass direction which would be seaward on the beach of origin, $\pm 60^\circ$; and are often within $\pm 30^\circ$ of this "correct" direction.

(4) The angle of orientation relative to the Moon changes appropriately, in at least a qualitative sense, with changes in the direc-

tion of the Moon. Some experimental series show close correspondence, and others relatively weak agreement, with inconsistencies between nights, but the changes are statistically significant in all experimental series for which quantitative data are available.

(5) In some cases, the animals have clearly shown appropriate changes in the angle of orientation during series of experiments conducted within a single night, but in other cases, no significant change in the angle during the night has been observed.

(6) In most experimental series, freshly-collected animals have shown some tendency to change their angle of orientation, for a given time of night, from one night to the next in an approximately appropriate manner to compensate for changes in day of the lunar cycle.

(7) Prolonged laboratory maintenance of the animals under constant conditions weakens the tendency for significant orientation to the Moon, and the orientations observed suggest that the capacity of the animals may deteriorate as to the choice of a direction which is at a constant angle from the azimuth of the Moon. Sometimes freshly collected animals show a similar tendency.

ACKNOWLEDGMENTS

The Naples experiments (Appendix 1) were performed during the tenure of a National Science Foundation postdoctoral fellowship; the Malibu experiments (Appendix 2) were supported by grant GB 2469 from the National Science Foundation; data analysis and preparation of this manuscript were supported by grant GB 5471 from the National Science Foundation. J. Aschoff offered his encouragement and support for the Naples experiments; Frau Ute Arch (née Wagner) gave technical assistance. Richard Swade and Ronald Quinn were of great help during the Malibu experiments. And finally, I must express my admiration for the accomplishment of F. Papi and L. Pardi in their discovery of Moon-compass orientation. I have, in this review, treated their data with cautious—and perhaps overly harsh—skepticism, but no reservations about specific aspects of their data can detract from the fact that, in my opinion, they were fundamentally correct in their initial interpretation. Friendly conversations and correspondence with them, as well as with A. Ercolini, have served to maintain my interest in talitrid orientation.

APPENDIX 1 *Naples Experiments*^a

| Date (1964) | Time (CET) | Lunar azimuth (deg) | Orientation azimuth (deg) | Vector length | Number of animals | Significance level | Days since collection | Lunar stage: days |
|-------------|------------|---------------------|---------------------------|---------------|-------------------|--------------------|-----------------------|-------------------|
| 3 IV | 21:41 | 217 | 201 | 0.81 | 16 | .01 | 1 | 9 |
| 3 IV | 22:18 | 231 | 227 | 0.92 | 11 | .01 | 1 | 9 |
| 3 IV | 23:00 | 244 | 211 | 0.63 | 25 | .01 | 1 | 9 |
| 3 IV | 23:20 | 251 | 240 | 0.65 | 24 | .01 | 1 | 9 |
| 4 IV | 00:09 | 259 | 249 | 0.38 | 25 | .05 | 1 | 9 |
| 4 IV | 01:25 | 272 | 242 | 0.53 | 25 | .01 | 1 | 9 |
| 4 IV | 01:58 | 276 | 258 | 0.79 | 17 | .01 | 1 | 9 |
| 8 IV | 21:26 | 130 | 160 | 0.33 | 22 | .05 | 3 | 14 |

APPENDIX 1.—(continued).

| Date (1964) | Time (CET) | Lunar azimuth (deg) | Orientation azimuth (deg) | Vector length | Number of animals | Significance level | Days since collection | Lunar stage: days |
|----------------|---------------|---------------------------|---------------------------------|------------------|----------------------|-----------------------|-----------------------------|-------------------------|
| 8 IV | 21:36 | 132 | 170 | 0.56 | 26 | .01 | 5 | 14 |
| 8 IV | 21:57 | 137 | 181 | 0.57 | 27 | .01 | 3 | 14 |
| 8 IV | 22:23 | 146 | 159 | 0.6 | 16 | .01 | 5 | 14 |
| 8 IV | 22:53 | 154 | 169 | 0.47 | 16 | .05 | 5 | 14 |
| 8 IV | 23:06 | 158 | 227 | 0.62 | 9 | .05 | 5 | 14 |
| 8 IV | 23:20 | 163 | 208 | 0.50 | 18 | .01 | 6 | 14 |
| 8 IV | 23:37 | 169 | 176 | 0.56 | 31 | .01 | 5 | 14 |
| 8 IV | 23:53 | 174 | 176 | 0.54 | 20 | .01 | 3 | 14 |
| 9 IV | 00:24 | 185 | 167 | 0.43 | 17 | .05 | 3 | 14 |
| 9 IV | 00:50 | 194 | 239 | 0.87 | 21 | .01 | 5 | 14 |
| 9 IV | 01:08 | 200 | 241 | 0.67 | 22 | .01 | 5 | 14 |
| 9 IV | 01:26 | 206 | 231 | 0.63 | 23 | .01 | 6 | 14 |
| 9 IV | 02:20 | 221 | 233 | 0.62 | 22 | .01 | 5 | 14 |
| 9 IV | 02:34 | 225 | 211 | 0.39 | 23 | .05 | 3 | 14 |
| 9 IV | 03:08 | 233 | 228 | 0.39 | 31 | .01 | 5 | 14 |
| 9 IV | 03:39 | 240 | 252 | 0.39 | 16 | .05 | 5 | 14 |
| 10 IV | 22:03 | 125 | 163 | 0.65 | 26 | .01 | 5 | 16 |
| 10 IV | 22:13 | 127 | 174 | 0.66 | 25 | .01 | 0 | 16 |
| 10 IV | 22:28 | 131 | 172 | 0.83 | 17 | .01 | 5 | 16 |
| 10 IV | 23:48 | 150 | 175 | 0.71 | 15 | .01 | 5 | 16 |
| 10 IV | 23:54 | 151 | 173 | 0.75 | 22 | .01 | 0 | 16 |
| 11 IV | 00:02 | 153 | 143 | 0.53 | 18 | .01 | 5 | 16 |
| 11 IV | 00:14 | 157 | 105 | 0.70 | 22 | .01 | 0 | 16 |
| 14 IV | 00:39 | 135 | 218 | 0.74 | 24 | .01 | 1 | 19 |
| 14 IV | 00:47 | 137 | 199 | 0.84 | 15 | .01 | 8 | 19 |
| 14 IV | 00:55 | 138 | 180 | 0.61 | 21 | .01 | 1 | 19 |
| 14 IV | 01:07 | 141 | 161 | 0.44 | 17 | .05 | 3 | 19 |
| 14 IV | 01:18 | 143 | 159 | 0.53 | 26 | .01 | 1 | 19 |
| 14 IV | 01:32 | 146 | 161 | 0.45 | 23 | .01 | 3 | 19 |
| 14 IV | 01:42 | 149 | 217 | 0.72 | 16 | .01 | 1 | 19 |
| 14 IV | 02:02 | 153 | 184 | 0.84 | 18 | .01 | 8 | 19 |
| 14 IV | 02:09 | 155 | 186 | 0.62 | 23 | .01 | 1 | 19 |
| 14 IV | 03:15 | 171 | 210 | 0.72 | 16 | .01 | 1 | 19 |
| 14 IV | 03:24 | 173 | 186 | 0.53 | 20 | .01 | 8 | 19 |
| 14 IV | 03:43 | 178 | 142 | 0.80 | 6 | .05 | 1 | 19 |
| 14 IV | 04:07 | 184 | 175 | 0.50 | 23 | .01 | 3 | 19 |
| 16 IV | 02:01 | 133 | 103 | 0.50 | 13 | .05 | 0 | 21 |
| 16 IV | 02:09 | 134 | 186 | 0.68 | 21 | .01 | 10 | 21 |
| 16 IV | 02:16 | 136 | 127 | 0.37 | 24 | .05 | 0 | 21 |
| 16 IV | 02:24 | 138 | 151 | 0.50 | 16 | .05 | 3 | 21 |
| 16 IV | 02:31 | 139 | 157 | 0.42 | 19 | .05 | 0 | 21 |
| 16 IV | 02:39 | 140 | 195 | 0.39 | 23 | .05 | 3 | 21 |
| 16 IV | 02:47 | 142 | 131 | 0.56 | 22 | .01 | 0 | 21 |
| 16 IV | 02:57 | 144 | 198 | 0.55 | 20 | .01 | 5 | 21 |
| 16 IV | 03:16 | 148 | 155 | 0.62 | 22 | .01 | 3 | 21 |

APPENDIX 1.—(concluded).

| Date (1964) | Time (CET) | Lunar azimuth (deg) | Orientation azimuth (deg) | Vector length | Number of animals | Significance level | Days since collection | Lunar stage: days |
|-------------|------------|---------------------|---------------------------|---------------|-------------------|--------------------|-----------------------|-------------------|
| 16 IV | 03:26 | 150 | 145 | 0.60 | 18 | 0.1 | 0 | 21 |
| 16 IV | 04:02 | 158 | 233 | 0.65 | 11 | .01 | 3 | 21 |
| 16 IV | 04:17 | 161 | 141 | 0.47 | 15 | .05 | 5 | 21 |

* Experimental animals (*Talitrus saltator*) were collected during daylight hours at several sites along the straight, continuous beach located about 40 km northwest of Naples. "Correct" orientation, perpendicular to that shore line, is at an azimuth of 235°. Experiments were conducted in a level open field about 1 km east of Lido di Licola. Nighttime air temperatures were between 5° C and 12° C. The observation chamber was heated in a water bath to 20 to 22° C, and a supply of CaCl₂ crystals, with color indicator, was within the chamber, which was about 30 cm in diameter and 5 cm deep, covered by a glass lid. Compass and clock were simultaneously photographed with the observation chamber, out of sight of the animals. All data are for second photographs, taken after the animals had been in the observation chamber for 5 min. Statistical significance evaluated by figure 15 of ref. 7; probability levels are not exact because of interactions between animals. Between collection and observation, the animals were stored at room temperatures in light-tight containers, including a strip of paper towel moistened with seawater.

APPENDIX 2
*Malibu Experiments**

| Date (1963) | Time (PST) | Lunar azimuth (deg) | Orientation azimuth (deg) | Vector length | Number of animals | Significance level | Days since collection | Lunar stage: days |
|-------------|------------|---------------------|---------------------------|---------------|-------------------|--------------------|-----------------------|-------------------|
| 20 VII | 21:28 | 184 | 205 | 0.73 | 20 | .01 | 0 | 10 |
| 20 VII | 21:36 | 187 | 204 | 0.55 | 18 | .01 | 0 | 10 |
| 20 VII | 21:53 | 191 | 201 | 0.74 | 21 | .01 | 0 | 10 |
| 20 VII | 22:08 | 195 | 185 | 0.54 | 25 | .01 | 0 | 10 |
| 20 VII | 22:18 | 198 | 166 | 0.58 | 23 | .01 | 0 | 10 |
| 20 VII | 22:30 | 201 | 183 | 0.65 | 29 | .01 | 0 | 10 |
| 20 VII | 22:46 | 205 | 189 | 0.80 | 20 | .01 | 0 | 10 |
| 20 VII | 22:58 | 208 | 178 | 0.59 | 20 | .01 | 0 | 10 |
| 20 VII | 23:14 | 211 | 174 | 0.46 | 26 | .01 | 0 | 10 |
| 20 VII | 23:25 | 214 | 179 | 0.61 | 24 | .01 | 0 | 10 |
| 20 VII | 23:36 | 216 | 185 | 0.89 | 27 | .01 | 0 | 10 |
| 20 VII | 23:45 | 218 | 166 | 0.48 | 27 | .01 | 0 | 10 |
| 20 VII | 23:55 | 220 | 194 | 0.52 | 27 | .01 | 0 | 10 |
| 21 VII | 00:18 | 225 | 167 | 0.60 | 11 | .05 | 0 | 10 |
| 21 VII | 00:28 | 227 | 184 | 0.68 | 23 | .01 | 0 | 10 |
| 21 VII | 00:38 | 229 | 215 | 0.66 | 12 | .01 | 0 | 10 |
| 21 VII | 00:48 | 231 | 120 | 0.56 | 23 | .01 | 0 | 10 |
| 21 VII | 00:57 | 232 | 159 | 0.68 | 25 | .01 | 0 | 10 |
| 21 VII | 01:04 | 233 | 176 | 0.68 | 28 | .01 | 0 | 10 |

APPENDIX 2.—(continued).

| Date (1963) | Time (PST) | Lunar azimuth (deg) | Orientation azimuth (deg) | Vector length | Number of animals | Significance level | Days since collection | Lunar stage: days |
|----------------|---------------|---------------------------|---------------------------------|------------------|----------------------|-----------------------|-----------------------------|-------------------------|
| 24 VII | 21:12 | 132 | 178 | 0.62 | 36 | .01 | 0 | 14 |
| 24 VII | 21:20 | 135 | 191 | 0.58 | 24 | .01 | 0 | 14 |
| 24 VII | 21:28 | 137 | 152 | 0.72 | 21 | .01 | 4 | 14 |
| 24 VII | 22:06 | 144 | 206 | 0.48 | 21 | .01 | 0 | 14 |
| 24 VII | 22:20 | 147 | 194 | 0.55 | 20 | .01 | 0 | 14 |
| 24 VII | 22:48 | 154 | 183 | 0.77 | 21 | .01 | 0 | 14 |
| 24 VII | 23:06 | 158 | 165 | 0.63 | 13 | .01 | 0 | 14 |
| 24 VII | 23:30 | 164 | 181 | 0.79 | 20 | .01 | 4 | 14 |
| 24 VII | 23:37 | 166 | 185 | 0.57 | 20 | .01 | 0 | 14 |
| 24 VII | 23:45 | 168 | 177 | 0.75 | 17 | .01 | 0 | 14 |
| 25 VII | 00:03 | 173 | 188 | 0.43 | 20 | .05 | 0 | 14 |
| 25 VII | 00:10 | 175 | 179 | 0.64 | 22 | .01 | 0 | 14 |
| 25 VII | 00:23 | 179 | 166 | 0.82 | 11 | .01 | 4 | 14 |
| 25 VII | 00:33 | 182 | 163 | 0.40 | 19 | .05 | 0 | 14 |
| 25 VII | 00:45 | 186 | 204 | 0.48 | 24 | .01 | 0 | 14 |
| 25 VII | 01:00 | 190 | 192 | 0.78 | 10 | .01 | 0 | 14 |
| 25 VII | 01:14 | 194 | 181 | 0.94 | 9 | .01 | 4 | 14 |
| 25 VII | 01:50 | 202 | 151 | 0.78 | 13 | .01 | 0 | 14 |
| 25 VII | 01:58 | 204 | 163 | 0.45 | 22 | .01 | 0 | 14 |
| 25 VII | 02:09 | 207 | 137 | 0.66 | 13 | .01 | 0 | 14 |
| 25 VII | 02:23 | 210 | 221 | 0.59 | 13 | .05 | 4 | 14 |
| 25 VII | 02:35 | 213 | 133 | 0.47 | 22 | .01 | 0 | 14 |
| 25 VII | 03:01 | 218 | 158 | 0.72 | 28 | .01 | 0 | 14 |
| 25 VII | 03:18 | 222 | 182 | 0.83 | 26 | .01 | 0 | 14 |
| 17 X | 18:53 | 137 | 206 | 0.59 | 23 | .01 | 3 | 10 |
| 17 X | 19:48 | 152 | 190 | 0.46 | 31 | .01 | 2 | 10 |
| 17 X | 20:06 | 157 | 180 | 0.67 | 26 | .01 | 2 | 10 |
| 17 X | 20:16 | 160 | 157 | 0.61 | 2 | .01 | 3 | 10 |
| 17 X | 20:26 | 163 | 163 | 0.63 | 19 | .01 | 2 | 10 |
| 17 X | 20:40 | 167 | 187 | 0.67 | 21 | .01 | 3 | 10 |
| 17 X | 20:55 | 172 | 201 | 0.68 | 19 | .01 | 2 | 10 |
| 17 X | 21:08 | 176 | 132 | 0.62 | 18 | .01 | 3 | 10 |
| 17 X | 21:21 | 180 | 159 | 0.67 | 26 | .01 | 2 | 10 |
| 17 X | 21:40 | 186 | 157 | 0.90 | 24 | .01 | 3 | 10 |
| 17 X | 21:53 | 191 | 180 | 0.75 | 20 | .01 | 2 | 10 |
| 17 X | 22:10 | 196 | 150 | 0.53 | 23 | .01 | 2 | 10 |
| 17 X | 22:22 | 200 | 164 | 0.78 | 25 | .01 | 3 | 10 |
| 17 X | 22:36 | 204 | 154 | 0.7 | 13 | .01 | 2 | 10 |
| 17 X | 22:56 | 210 | 184 | 0.70 | 22 | .01 | 3 | 10 |
| 17 X | 23:06 | 213 | 167 | 0.89 | 27 | .01 | 2 | 10 |
| 17 X | 23:36 | 221 | 166 | 0.70 | 18 | .01 | 3 | 10 |
| 17 X | 23:48 | 223 | 175 | 0.91 | 21 | .01 | 2 | 10 |
| 18 X | 00:00 | 226 | 152 | 0.52 | 12 | .05 | 3 | 10 |
| 18 X | 00:08 | 228 | 184 | 0.54 | 13 | .05 | 2 | 10 |
| 18 X | 00:20 | 231 | 199 | 0.77 | 20 | .01 | 2 | 10 |

APPENDIX 2.—(concluded).

| Date (1963) | Time (PST) | Lunar azimuth (deg) | Orientation azimuth (deg) | Vector length | Number of animals | Significance level | Days since collection | Lunar stage: days |
|-------------|------------|---------------------|---------------------------|---------------|-------------------|--------------------|-----------------------|-------------------|
| 18 X | 00:36 | 234 | 180 | 0.40 | 26 | .05 | 3 | 10 |
| 18 X | 00:51 | 237 | 178 | 0.35 | 30 | .05 | 2 | 10 |
| 18 X | 01:07 | 240 | 229 | 0.58 | 21 | .01 | 3 | 10 |
| 18 X | 01:18 | 242 | 209 | 0.61 | 7 | .01 | 2 | 10 |
| 18 X | 02:00 | 248 | 190 | 0.46 | 22 | .01 | 2 | 10 |

^a Experimental animals (*Orchestoidea corniculata*) were collected during daylight hours from east end of beach fronting on "The Colony" in Malibu, California. Correct orientation, perpendicular to that shoreline, is at an azimuth of 193°. Experiments were conducted atop the Biology Building at California State College, at Northridge, California. Nighttime air temperatures ranged from about 12° C to 18° C. For other experimental details, see footnote to Appendix 1.

APPENDIX 3

*Published Records of Non-significant^a Moon Orientation
by Talitrids*

PARDI AND PARDI; ref. 3:

Table 3, observations 3, 4, 6, 7, and 12

PARDI AND ERCOLINI; ref. 6:

Table 1a, observations 1, 2, 3, 4, 6, 7, and 12

Table 1b, observations 4, 5, 14, and 17

Table 2a, observations 2, 3, 4, and 5

Table 2b, observations 1 and 2

Table 3a, observations 4 and 5

Table 3b, observations 4, 5, 6, 7, and 8

^a Vector length not different, at 0.05 level (see footnote 3 in text) from random scatter on the basis of numbers of animals used. Number of animals determined by dividing number of record positions by number of photographs or counts.

APPENDIX 4

*Visual Observations of Orientation Which Apparently Are Duplicate
Measurements of the Same Animals Previously Photographed*

PARDI AND ERCOLINI; ref. 6:

Table 1a, observations 5, 7, 9, 11, 13, and 15

Table 1b, observations 5, 7, 9, 11, 13, 15, 17, and 19

DISCUSSION

LINDAUER: Have you more information concerning the experience of animals prior to testing? How long has an animal to see or to learn the Moon movement across the sky until he is familiar with this?

ENRIGHT: One aspect of this hypothesis, which does make it testable, is the proposition that if animals are kept under constant conditions in the laboratory for a period of two weeks or longer, then they should show only the constant-angle orientation, and show no evidence for time compensation in the orientation, as contrasted with freshly collected animals. This is consistent with the few data which are available. It is also true, however, that animals that have been kept in the laboratory for a longer period of time are less likely to show any consistent choice of direction and one must distinguish between these two.

SHOOP: Do you have any data on individual behavior as related to group behavior? Do individuals respond as groups do? Are these all group data that you presented?

ENRIGHT: These are all group data. My own qualitative impression is that the animals do not influence each other's choice of direction very much even though they crawl over and bump into each other occasionally.

GRIFFIN: Is it true that the animals oriented in the opposite way under water?

ENRIGHT: Yes, but there was no claim for this with regard to the Moon compass orientation. The reverse orientation was claimed only for Sun orientation, and I have been unable to reproduce this observation. Animals actually swimming in sea water seem to orient in the same direction as those in a dry chamber. There is an additional complication. It is now claimed in the literature that talitrids orient in the same direction as they do in a dry chamber, if you put them in fresh water; it is only in salt water that they orient away from the beach.

WALCOTT: What would be the consequence in the orientation if your animals were using a time clock based on the Sun rather than on the Moon?

ENRIGHT: It would vary from night to night, and hour to hour.

BULLOCK: Curt Richter cites many cases of rhythm in humans which are only manifested after some kind of clinical experience that he regards as a shock. In other words, he supposes that the endogenous clock is there, but it is not a single clock. It is a lot of independently phased cells, which are in-

dividually going along at the normal rate, but out of step with each other. Some special environmental trigger, which he calls clinical shock in the human patients, brings all these cells into synchronization so that they can take control of the organism and the rhythm then becomes manifest in overt signs.

ENRIGHT: I have difficulty imagining what the environmental trigger could be.

BULLOCK: Might it be moonrise or is it the time the animal emerges from the sand?

ENRIGHT: I have a hard time imagining how Moon synchronization of this kind of a clock would work, even though I have proposed the hypothesis.

BULLOCK: Put it the other way around. It is the cold or the fog that lets the cells, the numerous endogenous clocks that have the same intrinsic rhythm, drift apart. When the animal can see the environmental sign, all his endogenous clocks get into synchrony, so that they, in your words, take control.

WATERMAN: Why do you assume that the Moon rather than the tides synchronizes this rhythm?

ENRIGHT: On the Pacific coast the tidal factors could represent a very good synchronizing agent for some sort of a lunar rhythmicity. The best argument against this, however, is that tides in the Mediterranean area are of very small amplitude and the animals live so far up the beach that direct experience of the tides seems unlikely.

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